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Influence of Drilling Muds on the Primary Chemosensory Neurons in Walking Legs of the Lobster, 'Homarus americanus'

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16. ABSTRACT

Tne effects of whole drillingmuds on the normal activity of walking leg chemosensory neurons were examined using extracellular neurophysiological recording techniques. Exposure of legs for 3-5 min to 10-mg/L drilling mud suspended in sea water altered responses to food odors of 29% of the chemoreceptors examined (data polled for the two drilling muds tested); similar exposure to 100-mg/L drilling mud resulted in interference with 44% of all receptors studies. The effects of both of these concentrations are statistically significant, although they are not different from each other. Interference was usually manifested as a marked reduction in the number of action potentials in a response. In one preparation, the exposure to drilling mud caused a change in the temporal pattern of the spikes without affecting the total number of spikes. Other chemosensory neurons were excited by 10-mg/L drilling mud itself. However, not all chemoreceptors are affected by these drilling muds since responses to feeding stimuli were recorded from the legs of lobsters that had been exposed to drilling mud for 4-8 d befor the neurophysiological experiments.

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Influence of Drilling Muds on the Primary Chemosensory Neurons in Walking Legs of the Lobster, *Homarus americanus*

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DERBY, C. D., AND J. ATEMA. 1981. Influence of drilling muds on the primary chemosensory neurons in walking legs of the lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 38: 268–274.

The effects of whole drilling muds on the normal activity of walking leg chemosensory neurons of the lobster, *Homarus americanus*, were examined using extracellular neurophysiological recording techniques. Exposure of legs for 3–5 min to 10 mg/L drilling mud suspended in seawater altered responses to food odors of 29% of the chemoreceptors examined (data pooled for the two drilling muds tested); similar exposure to 100 mg/L drilling mud resulted in interference with 44% of all receptors studied. The effects of both of these concentrations are statistically significant, although they are not different from each other. Interference was usually manifested as a marked reduction in the number of action potentials in a response. In one preparation, the exposure to drilling mud caused a change in the temporal pattern of the spikes without affecting the total number of spikes. Other chemosensory neurons were excited by 10 mg/L drilling mud itself. However, not all chemoreceptors are inhibited by these drilling muds since responses to feeding stimuli were recorded from the legs of lobsters that had been exposed to drilling mud for 4–8 d before the neurophysiological experiments.

Antennular and leg chemoreceptors are important in eliciting normal feeding behavior in lobsters. Although behavioral assays have demonstrated that feeding behavior is altered following exposure to drilling muds and petroleum fractions, there is no conclusive proof for a causal relationship between chemoreceptor interference and behavioral deficits. The two techniques complement each other as pollution detection assays, perhaps reflecting a common interference mechanism.

Key words: chemoreception, drilling mud, feeding behavior, lobster, pollution, neurophysiology

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Des méthodes d'enregistrement neurophysiologiques extracellulaires ont servi à étudier les effets des vases de forage sur l'activité normale des neurons chimiosensoriels des pattes ambulatoires du homard, *Homarus americanus*. Une exposition des pattes durant 3–5 min à 10 mg/L de vase de forage en suspension dans de l'eau de mer influe sur les réponses à des odeurs de nourriture de 29% des chimiorécepteurs examinés (groupage des données des deux vases de forage testées); une semblable exposition à 100 mg/L de vase de forage produit une interférence dans 44% de tous les récepteurs étudiés. Bien que les effets de l'une et l'autre de ces concentrations ne diffèrent pas entre eux, ils sont significatifs à l'analyse statistique. L'interférence se manifeste ordinairement par une diminution marquée du nombre des potentiels d'action dans une réponse. Dans une préparation, l'exposition à la vase de forage produit un changement dans le schéma temporel des crêtes, sans agir sur le nombre total de ces dernières. D'autres neurons chimiosensoriels sont excités par 10 mg/L de vase de forage seule. Cependant, ce ne sont pas tous les chimiorécepteurs qui sont influencés par ces vases de forage puisqu'on a enregistré des réponses à des stimuli alimentaires sur des pattes de homards qui avaient été exposés à de la vase de forage pendant 4–8 d avant les essais neurophysiologiques.

Un rôle important des chimiorécepteurs des antennules et des pattes est de provoquer le comportement alimentaire normal chez les homards. Bien que des expériences sur le compor-

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tement aient démontré que le comportement alimentaire change après exposition aux vases de forage et aux fractions d'hydrocarbures, il n'y a pas de preuve définitive d'une relation causale entre l'interférence subie par les chimiorécepteurs et un comportement aberrant. Les deux types d'expériences se complètent comme méthodes analytiques de détection de la pollution, signe possible d'un mécanisme d'interférence commun.

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DRILLING muds (drilling fluids) are a group of potentially hazardous pollutants. Drilling muds are mixtures of clays, water, and chemical additives used during oil and gas drilling operations to lubricate the bit, remove drilled cuttings, and equalize hydrostatic pressure. The drilling muds are continually released into the surrounding waters during the drilling operation and, in addition, are released in bulk upon completion of the drilling operation. The compositions of drilling muds vary, but they often contain suspended drilled solids, weighting agents (barite, bentonite clays), viscosifiers (chromium lignosulfonates), fluid-loss reducers, flocculants, dispersants, detergents, surfactants, defoamers, emulsifiers, lubricants (processed hydrocarbons), bactericides (sodium pentachlorophenate), and alkaline compounds (Land 1974; Wright 1975). Whole drilling muds or individual components of drilling muds have caused sublethal and lethal effects on marine organisms (e.g. Thompson and Bright 1977; Tagatz et al. 1978; Rao et al. 1979; Conklin et al. 1980), including lobsters (S. Oleszko-Szuts, J. Atema, E. Karnofsky, and R. Elgin, 1979, unpublished data).

Chemoreception is probably the dominant sensory modality with which lobsters and most other benthic organisms relate to their environment, using it to obtain food (Ameyaw-Akumfi 1977; Hirtle and Mann 1978; Reeder and Ache 1980) and mates (McLeese 1970; Atema and Engstrom 1971; Gleeson 1980). Various chemical pollutants, including such potential components of drilling muds as surfactants, detergents, dispersants, and petroleum, are known to affect adversely chemically mediated behaviors of many marine organisms, including bacteria, invertebrates, and vertebrates. Petroleum inhibits bacterial chemotaxis (Walsh and Mitchell 1973). Such chemically elicited behaviors of crustaceans as pheromone detection and food detection, location, and consumption can be interfered with by different pollutants (Swedmark et al. 1971; Takahashi and Kittredge 1973; Milovidova 1974; Evans et al. 1977; Lyes 1979). In addition, the feeding behavior of both larval (Wells and Sprague 1976) and adult (Atema and Stein 1974; Atema 1976; Atema et al. 1979b) lobsters can be deleteriously affected by the water-soluble and water-accommodated fractions of petroleum.

It has been assumed in many of these studies that interference takes place at the primary sensory receptors themselves; however, this assumption has rarely been examined. The structure and function of chemoreceptors of some fish may be impaired by detergents and certain ionic surfactants (Bardach et al. 1965; Sutterlin et al. 1971). Neurophysiological experiments with chemoreceptors in lateral flagella of antennules of *H. americanus* indicate that 1–10 mg/L No. 2 fuel oil added to a mussel extract causes nerve-firing patterns different from those elicited by the mussel extract alone (Atema et al. 1979b).

Direct pollutant effects on the chemoreception process can be measured by a neurophysiological test such as is described here. Chemoreceptors in the legs are of particular interest since they are heavily exposed when the pollutant is part of the substrate, as is the case with drilling muds. The experiments presented here demonstrate that a short-term exposure of 10- or 100-mg/L drilling mud can interfere with the normal physiological activity of the primary chemosensory cells in the walking legs of the lobster, *H. americanus*.

Materials and Methods

The effects of short-term exposure of whole drilling muds (DM) on the physiology of primary sensory neurons were examined by recording neurophysiological responses from chemoreceptors in the walking legs of lobsters. Two types of drilling muds were tested: "DM-2" (density = 1.14 g/mL, pH = 11) and "DM-3" (density = 1.51 g/mL, pH = 11), both collected from wells in Mobile Bay, Gulf of Mexico, and supplied by Dr Norman L. Richards, U.S. Environmental Protection Agency, Environmental Research Laboratory, Gulf Breeze, Florida.

Legs from two groups of lobsters were tested: "clean" lobsters and "DM-treated" lobsters. All animals were individually held in 100-L aquaria with a flow-through seawater system and a 5-cm layer of sand covering the bottom. DM-treated lobsters received a single introduction of 100- or 1000-mL DM (resulting in a 1- to 10-mm layer of DM on top of the sand) 4–8 d before the neurophysiological experiments were performed. They were treated in the aquaria and tested in the neurophysiological experiments with the same type of DM. Clean lobsters did not receive this 4- to 8-d DM treatment.

Neurophysiological experiments were performed on the walking legs of these lobsters. After a leg was removed from a lobster, the exoskeleton of all but the two most distal segments (dactylus and propodus) was carefully dissected away, exposing the sensory nerve bundle. These two remaining intact segments were inserted through a rubber dam in a Plexiglas chamber (modified from the design for antennules described by Atema et al. 1979b) so that this leg section was isolated from the exposed nerve. The nerve was bathed in *Homarus* Ringer's solution, and a constant stream of filtered seawater (10 mL/min) flowed over the distal leg region. Chemical stimuli (50 μL) were injected into this flow, and neural responses from chemoreceptors that had been separated from the main sensory nerve bundles were recorded extracellularly with a platinum hook electrode. Two chemical stimuli known to activate lobster chemoreceptors strongly

TABLE 1. Protocol for analysis of short-term effects of drilling muds.

Background flow[a]
1. FSW
2. 10 mg/L DM
3. FSW
4. 10 mg/L DM
5. FSW
6. 100 mg/L DM
7. FSW
8. 100 mg/L DM
9. FSW

[a]The legs were exposed to each background flow for 3–5 min before the responses to at least two presentations of each of the following were recorded: L-glutamate, mussel extract, and filtered seawater (FSW). For DM-2, backgrounds 1–5 were tested; for DM-3, backgrounds 1–9 were tested.

(Derby and Atema 1978) were used: mussel (*Mytilus edulis*) extract (100 mg tissue/L filtered seawater) and 10^{-5} mol/L L-glutamate. The introduced chemical stimuli were diluted in the chamber by a factor of 30 when they reached the leg receptors, as determined independently by spectrophotometric measurements following dye injection and by measuring conductance changes following injection of a salt solution. The reported concentrations of introduced stimuli include this dilution factor.

In one set of experiments, responses to an addition of 50 μL of 10 mg/L DM were recorded from chemoreceptors of clean and DM-treated lobsters to determine if DM itself can stimulate chemoreceptors in the legs. In a second set of experiments, short-term effects of DM were tested by monitoring the chemoreceptor responses to the following stimuli: L-glutamate, mussel extract, and filtered seawater (control stimulus). These stimuli were presented in three different background flows: filtered seawater (FSW), 10 mg/L DM in FSW, or 100 mg/L DM in FSW. The protocol used is described in Table 1. A loss of response to food odors following the exposure to DM could be due either to an effect of DM on the neurons or to a recording problem with the neurophysiological preparation (e.g. loss of neuron-to-electrode contact). Therefore, to ensure that the effect was due only to DM, the entire set of recordings was voided if the response to the food odor was not retrieved following a period of rinsing with FSW. Recordings were made from only one nerve bundle per leg to avoid effects of previous exposure on subsequent tests. For DM-2, responses were recorded from seven legs of five clean lobsters and from seven legs of six DM-treated lobsters. For DM-3, responses were recorded from 11 legs of eight clean lobsters and 13 legs of six DM-treated lobsters. Neural activity was amplified on standard electrophysiological equipment and stored on magnetic tape for subsequent analysis.

Results

Introduction of 50 μL of a 10-mg/L drilling mud (DM) stimulus into the FSW background flow elicited responses (e.g. Fig. 1), whereas control stimuli (FSW) did not, demonstrating that DM itself can be sensed by chemoreceptors. No

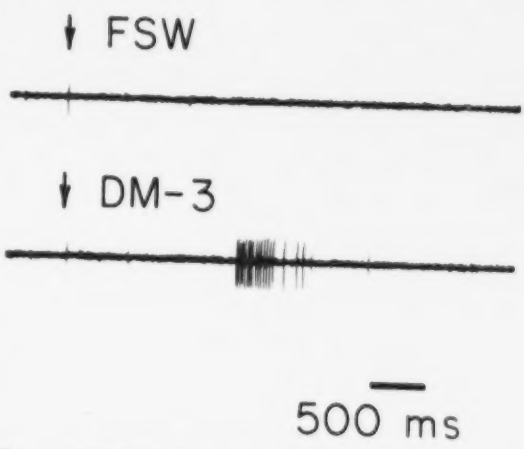

FIG. 1. Detection of 10 mg/L DM-3 stimulus by chemoreceptor on leg of DM-treated lobster. Arrow indicates stimulus introduction.

chemoreceptors of clean lobsters responded to DM-2, but 17% responded to DM-3; 20% of the chemoreceptors of DM-treated lobsters responded to DM-2, while 46% responded to DM-3 (Table 2). The difference between responses to 10 mg/L DM stimuli and to filtered seawater stimuli is significant ($P < 0.05$, sign test; data pooled for DM-2 and DM-3 and for clean and DM-treated lobsters).

Short-term exposure to DM-2 and DM-3 caused interference of the responses to food odors. Interference is defined as a clear reduction in the total number of action potentials (spikes) in the response to either L-glutamate or mussel extract during exposure to drilling mud as compared to the response before and after exposure. Representative examples of such interference caused by DM are illustrated in Fig. 2 and 3. In one case, rather than reducing the number of spikes elicited by the mussel extract stimulus, the exposure to DM caused a clear and reproducible modification of the temporal pattern of the spikes (Fig. 4). This change in response pattern is considered to be an interference effect caused by DM. Figure 4 is an example of the reproducibility of responses to repeated introductions of the same stimulus. Short-term exposure to 10 mg/L DM-2 caused interference in 57% of the clean lobsters (Fig. 2), but not in 4- to 8-d DM-treated lobsters. Short-term exposure to 10 mg/L DM-3 caused interference in 18% of the clean lobsters and in 44% of the DM-treated lobsters (Fig. 4). Exposure to 100 mg/L DM-3 caused interference in 50% of the clean lobsters (Fig. 3) and 38% of the DM-treated lobsters (Fig. 4). The results are summarized in Table 2. The sign test (Siegel 1956) demonstrates that the interference effects of both 10- and 100-mg/L DM-3 are statistically significant (both $P < 0.05$; data pooled for clean and DM-treated lobsters), and that while the effect of 10 mg/L DM-2 does not reach this probability level, it does show a similar trend ($P = 0.06$). The Fisher exact probability test finds no significant difference ($P < 0.05$) between the effects of 10- and 100-mg/L DM.

Discussion

Examination of the activity of chemosensory neurons is an

TABLE 2. Effect of drilling muds on chemoreceptors: (A) excitation and (B) interference of responses to food odors.

Treatment of lobsters previous to neurophysiological test[a]	Type of DM	Excitation	Interference of responses to food odors	
			10 mg/L DM	100 mg/L DM
Clean lobsters	DM-2	0/5[b] (0.0%)	4/7[c] (57.1%)	—
	DM-3	1/6 (16.7%)	2/11 (18.2%)	4/8 (50.0%)
DM-treated lobsters	DM-2	1/5 (20.0%)	0/7 (0.0%)	—
	DM-3	6/13 (46.1%)	4/9 (44.4%)	3/8 (37.5%)

[a]See Materials and Methods for explanation of treatments.
[b]The ratio of the number of chemoreceptors responding to a 10-mg/L DM stimulus and the number of chemoreceptors tested.
[c]The ratio of the number of chemoreceptors in which the response to the food odor was clearly altered by DM and the number of chemoreceptors tested. Dashes signify that this DM concentration was not tested.

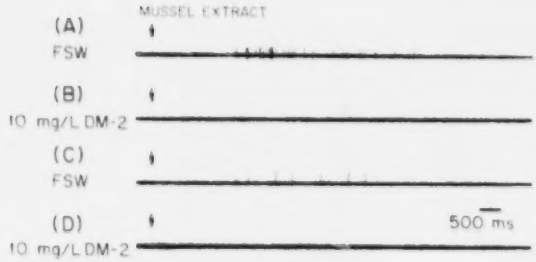

FIG. 2. Complete inhibition of clean lobster leg chemoreceptor response to mussel extract stimulus by DM-2. Mussel extract was introduced into the following background flows: (A) FSW; (B) 10 mg/L DM; (C) FSW; (D) 10 mg/L DM. Arrows indicate stimulus introduction.

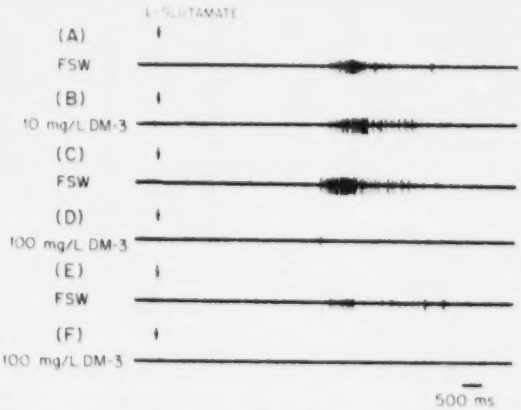

FIG. 3. Inhibition of clean lobster leg chemoreceptor response to 10^{-5} mol/L L-glutamate stimulus by DM-3. L-Glutamate was introduced into the following background flows: (A) FSW; (B) 10 mg/L DM; (C) FSW; (D) 100 mg/L DM; (E) FSW; (F) 100 mg/L DM. Arrows indicate stimulus introduction.

effective method of monitoring the influence of drilling muds on chemoreception. Reproducible results of drilling mud-induced changes of the responses of chemoreceptors to feeding stimuli have been obtained: a 3–5-min exposure to 10- or 100-mg/L whole used drilling mud altered the normal activity of 33 and 50%, respectively, of the leg chemoreceptors of all clean lobsters examined (Fig. 2–4; Table 2). In addition, 25 and 37.5% of the chemoreceptors in legs of long-term treated (4–8 d) lobsters were inhibited by 10- and 100-mg/L drilling muds, respectively. However, normally functioning receptors were found in these drilling mud-treated lobsters, indicating that not all chemoreceptors are altered by such long-term drilling mud treatments. It has also been demonstrated that there are chemosensory neurons on the walking legs that respond to drilling mud itself. Drilling mud excited chemoreceptors in 28% of all nerve bundles that responded to either a mussel extract or L-glutamate (Fig. 1; Table 2). The possible behavioral consequences of these sensory physiological effects are discussed later.

It is not known which components of drilling muds directly excite certain chemoreceptors or which components inhibit the responses of other chemoreceptors to feeding stimuli. Nor has the cellular mechanism of this interference been determined in this study. Structural damage of chemoreceptors following exposure to pollutants can occur in some aquatic species (Bardach et al. 1965), although there is no evidence that oil causes changes in the gross cellular morphology of antennular chemoreceptors of lobsters (Atema and Stein 1974). The interference could possibly result from a physical blockage of the receptor surfaces so that odorant molecules cannot reach the receptor sites on the chemoreceptor membrane surface. A more likely possibility, however, is that some components of the drilling muds are complexing with the membrane lipids (Hodgson and Steinhardt 1967; Kaissling 1977) and/or proteins (Manwell and Baker 1967; Boldacre 1968), thus disrupting the transduction process (Poynder 1974).

Behavioral consequences of these effects of drilling muds on chemoreceptor function are not known, but parallel behavioral experiments indicate that adult lobsters held in a flow-through system show suppressed or abnormal feeding behavior when exposed to a 1-mm layer of certain types of drilling muds (Oleszko-Szuts et al., 1979, unpublished data). These results are in agreement with oil-induced changes in chemoreception and feeding behavior of lobsters (Atema 1976; Atema et al. 1979b). Numerous behavioral studies have demonstrated that other decapod crustaceans can also detect chemical pollutants and may respond with avoidance, attrac-

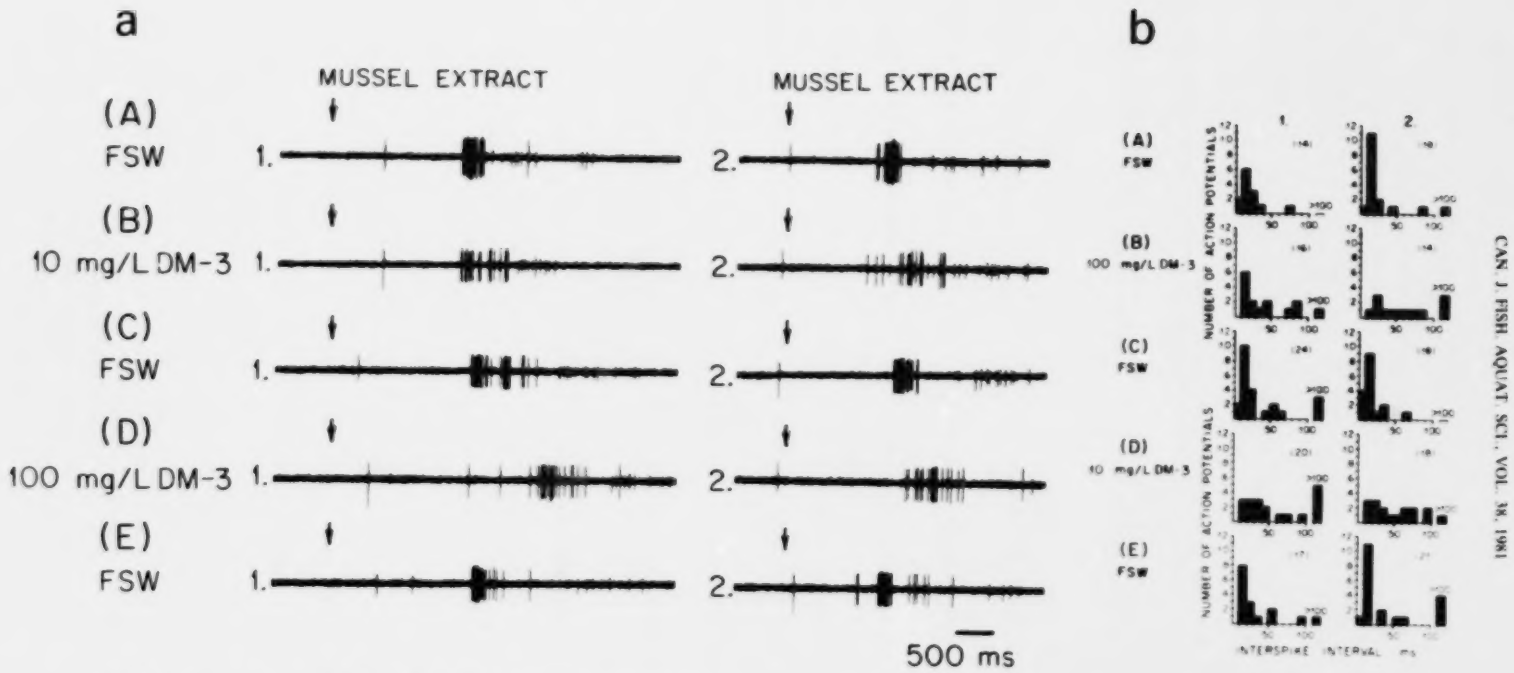

FIG. 4. Change in temporal pattern of DM-treated lobster leg chemoreceptor response to mussel extract stimulus by DM-3. (a) Recorded responses; (b) spike interval histograms of recorded responses. Mussel extract was introduced twice into each of the following background flows: (A) FSW; (B) 10 mg/L DM; (C) FSW; (D) 100 mg/L DM; (E) FSW. Both 10- and 100-mg/L DM caused increases in the mean interspike interval (spike pattern), but no reduction in number of spikes per response. The numbers in parentheses represent the total number of spikes per response.

tion, or ambiguous behavior (Percy 1976; Zimmer et al. 1979; Pearson and Olla 1979, 1980; Pearson et al. 1980, 1981).

Drilling muds can be toxic to marine crustaceans at concentrations near those used in these neurophysiological experiments. Conklin et al. (1980) examined the effects of 18 different drilling muds on two crustacean species, the grass shrimp *Palaemonetes pugio* and the mysid *Mysidopsis bahia*. When intermolt individuals of *P. pugio* were exposed to 100 mg/L drilling mud during 96-h bioassays, one mud caused 100% mortality and six caused 30–60% mortality. However, both of these species were found to be more susceptible to drilling muds during molting: 150 mg/L caused 10% mortality of *P. pugio*; for *M. bahia*, the LC_{50} for one mud was 50 mg/L, and even at 10 mg/L there was 5–25% mortality. The toxic effects of drilling muds on adult lobsters also depend on the type of drilling mud: a single dumping of one type of drilling mud, enough to form a 10-mm layer on the substrate, was lethal within 4 h of introduction (Oleszko-Szuts et al., 1979, unpublished data); other muds are less toxic (Atema personal observations).

The likelihood that marine animals in their natural habitat will be exposed to concentrations of drilling muds comparable to those used in these experiments is an important question. Dilution and dispersion rates of drilling muds released into oceanic waters are difficult to estimate since these rates depend on such variables as local atmospheric and hydrographic conditions, position of outfall with respect to the ocean bottom, and composition of drilling muds. Mariani et al. (1980), in studying the chemical and physical alterations in the benthic environment following release of drilling muds from a well off the mid-Atlantic outer continental shelf, state that most of these changes occurred within a 3-km radius of the well site. A model for a well in the Gulf of Mexico (Ray and Shinn 1975) predicts that full concentration drilling mud released at 40 bbl/h would be diluted in the open water to 1000 mg/L suspended load at 0.3 km and to 100 mg/L at 3 km downstream from the discharge; for a release rate of 250 bbl/h, a concentration of 1000 mg/L would occur in the water at 3 km downstream. However, the fact that plumes of drilling muds are often visible 4–5 km downstream from the release site (Bureau of Land Management 1979) indicates that exposure to certain components of drilling muds may be more widespread than the above studies describe. It is uncertain if it is the particulate or the soluble fraction of drilling mud which is most toxic to animals. Although many studies deal with drilling muds in solution/suspension, the amount of drilling mud covering the substrate may be an equally or more important factor for benthic animals such as adult lobsters. Under such conditions, the chemoreceptors on their legs would be chronically and directly exposed to the drilling mud.

Chemoreception is important for the ability of crustaceans to obtain such resources as mates (Atema and Engstrom 1971; Atema et al. 1979a; Gleeson 1980) and food (McLeese 1970; Reeder and Ache 1980). The sensory input from chemoreceptors on the walking legs is essential in eliciting the normal sequence of feeding behaviors (Maynard and Sallee 1970); without this input, the ability of crustaceans to locate and grasp food items is greatly impaired (Ameyaw-Akumfi 1977; Derby personal observations). Interference of the chemoreceptive systems by such pollutants as drilling muds may subsequently have consequences on the fitness of exposed animals during competition for resources.

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